The natural history of nesting in two Australian freshwater turtles.

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ABSTRACT

The nesting behaviour of two Australian freshwater turtles, the broad-shelled river turtle *Chelodina expansa* and the Brisbane river turtle *Emydura signata* are described.

Both species nest during, or soon after rain. *C. expansa* nests exclusively during the day while *E. signata* as a preference for nesting at night but can be found nesting during the day. *C. expansa* nests 30-300 m from the water's edge usually after walking up a hill, while *E. signata* typical nests just 2-10 m from the water's edge. Both species dig their nests exclusively with their hind legs by alternative scooping movements. Nest excavation takes from 20 to 180 minutes depending on how hard the soil is compacted. Typically some water is released from the cloaca during the nesting process but the role of this behaviour remains unknown. *C. expansa* uses a 'body-slamming' behaviour to compact the nest plug at the end of nesting but this behaviour was not observed in *E. signata*.

Key words: nesting, turtles, oviposition,

Introduction

Turtles in general have a stereotypic nesting and egg-laying behaviour (Ehrenfeld 1979; Kuchling 1993). This usually involves leaving the water, finding a nesting site, preparation of the nest site, digging the nest with the back legs, laying eggs into the nest, back-filling the nest, and then finding their way back to the water (Ehrenfield 1979). However there are inter-species variations in this general behaviour pattern, the most notable being the underwater nesting behaviour of the Australian northern long-necked turtle *Chelodina rugosa* (Kennett et al. 1993) and the use of the front feet to dig the nest in the Australian western swamp turtle *Pseudemydura umbrina* (Kuchling 1993). However there are surprising few detailed observations of nesting behaviour in freshwater turtles, and to date only anecdotal natural history notes on Australian species (Curtis 1928; Goode 1965; Vestjens 1969; Clay 1981). These observations have typically been made on only one or two individuals. To help fill this gap in our knowledge of this aspect of Australian freshwater turtle biology, I report on the nesting and ovipostion behaviour of two Australian freshwater turtles, the Brisbane river turtle *Emydura signata* and the broad-shelled river turtle *Chelodina expansa*. These observations have been made on an opportunistic basis over a number of years while collecting data for other projects.

Methods

All observations were made on turtles emerging to nest from a populations inhabiting artificial lakes constructed in 1962 on the St Lucia campus of The University of Queensland, Australia (27°32'S, 153°00'E). This area consists of two small (~400m^2) and one larger (~2000m^2) lakes which are surrounded my mown grass and pedestrian paths. The topography of the land to the east of the lakes slopes gently upwards (~1 in 10m rise), while the land to the west is considerably steeper (~1 in 5m rise). The soil surrounding the lakes has a large clay component and is infiltrated with small stones (~2-5mm in diameter) and becomes very hard when dried out.

During the autumn and summer of 1993, regular daily searching for newly constructed nests revealed that nesting only ever occurred during or after rain, so in subsequent years nesting activity was only searched for during or immediately after rain. During 1994 and 1995 these searches occurred during the day and night during both the *E. signata* and *C. expansa* nesting seasons. However, because *C. expansa* was never found nesting during the night, night-time searches were ceased during the *C. expansa* nesting season from 1996 onwards. If a turtle was found on land during these searches it was caught and marked by marginal scute mutilation.

When time permitted, detailed observations of nesting behaviour were made from a distance of 15-20 m for *E. signata* and 5-10 m for *C. expansa*. During these observations a watch was used to record the time taken to complete the various stages of nesting behaviour. The straight line distance from the nest to the water's edge was measured with a 100 m measuring tape for 18 *E. signata* nests and 12 *C. expansa* nests.

Results are reported as means and standard errors of the means. Comparisons between species were made using student-t tests.

Results

Since 1993 a total of 28 female *C. expansa* and 125 female *E. signata* have been marked. Between 1993 and 2008, 219 *E. signata* and 107 *C. expansa* were noted out of the water exhibiting nesting behaviour. The full nesting behaviour from the time of first emergence from water to re-entering the water of six *C. expansa* and ten *E. signata* was observed and the time taken for each of the nesting stages noted.

Nesting season

Both *E. signata* and *C. expansa* were only ever observed out of the water nesting after or during rain. *C. expansa* is an Autumn-Winter nester with nesting activity observed between 19 February through to 6 November, but most nesting events occurred between March and June with a Julian (from 1 January) mean of 127 ± 8 d (Fig. 1). *E. Signata* is a Spring-Summer nester with nesting activity observed between 12 September and 23 January, but almost all nesting events occurring between September and November with a Julian mean of 208 ± 5 d (Fig. 1). The mean Julian day of laying for *E. signata* and *C. expansa* were significantly different ($P < 0.001$).

Nest site selection

C. expansa was never observed nesting after dark, but could be found nesting at any time during daylight. The average time from emergence from water to the beginning of nest construction was 34 ± 5 min (range 20-60 min) and sometimes nest digging at the first site selected was abandoned before moving off and completing a nest at another site. When this happened turtles typically moved several metres and started nest digging again or occasionally abandoned nesting activity and returned to the water without laying eggs. *C. expansa* females almost always walked up hill away from the water to choose a nest site located on average 120 ± 26 m (range 30-300 m) from the water's edge. This species was very tolerant of pedestrian traffic and as long as they were not touched continued up hill to the favoured nesting areas despite being approached by curious people. Once up a hill, turtles did not appear to actively choose a particular ground condition or soil type into which to nest, although all areas were open being regularly mown grass for bare earth. Turtles were able to dig into heavy clay soils. On several occasions turtles constructed their nests in the highly compacted soil in the middle of pedestrian paths.

E. signata was observed to nest most frequently in the first few hours after dark, although could also be found nesting at all times of the day. If nesting during day light, nesting was most frequent during early morning or late afternoon. The average time from emergence from water to the beginning of nest construction was 14 ± 3 min (range 5-30 min) and sometimes nest digging at the first site selected was abandoned before a nest was completed. When this happened turtles typically moved several metres and started nest digging again or occasionally abandoned nesting activity and returned to the water without laying eggs. *E. signata* took significantly less time ($P < 0.005$) than *C. expansa* to begin nest construction. *E. signata* was very timid and would turn and flee back into the water if approached by pedestrians. *E. signata* typically constructed their nests within 2-10 m from the water's edge (mean 4.3 ± 0.6 m), but occasional an individual would nest up to 50 m away. *E. signata* nested significantly closer (Student- t test adjusted for unequal variances, $P = 0.001$) to the water's edge than *C. expansa*.

When moving from the water to a nesting site, both *C. expansa* and *E. signata* proceed at a slow walk. Some individuals stop every few metres and appear to look around before proceeding forward again, but others marched on continuously. When collected on the way to nesting sites, both species frequently had water stored in their bladder/cloaca and this could be released immediately on being picked up or at some later date (I routinely took turtles to be X-rayed at this stage and water was released up to 5 hours after collection).

Nest construction

Neither *C. expansa* nor *E. signata* prepare the nest site for construction, no clearing with front or back feet was ever observed. In both species nest excavation was done by alternate scooping by the hind feet. One foot scooped out some soil that was put to one side, and then the other foot scooped out some soil and that was put to the other side (Fig. 2). As the nesting hole became deeper there would be periods of up to 5 minutes between the alternate scooping of the feet. In some cases it appeared that water stored in the cloaca or bladder was emptied into the nest (as judged

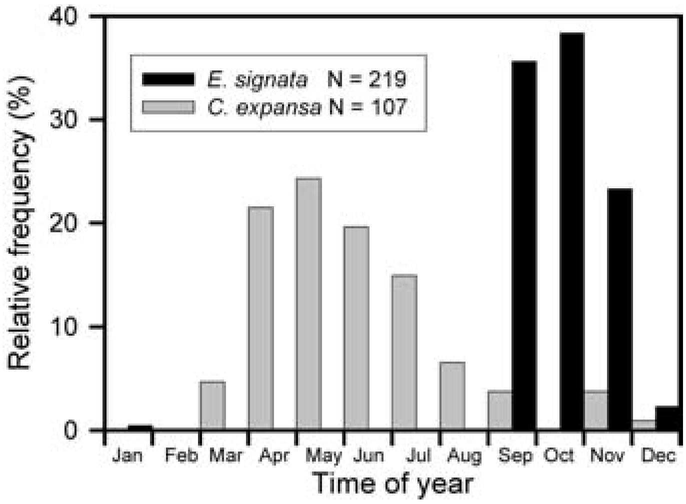

Figure 1. Relative frequency of nesting events for the University of Queensland St Lucia's population of broad-shelled river turtle (*C. expansa*) and Brisbane river turtle (*E. signata*).

Figure 2. Nest construction in the broad-shelled river turtle *Chelodina expana.* One hind foot at a time is inserted into the nest to scoop out the soil.

by an increase in water content of soil in relatively dry soil) but I never observed this water actually exiting the cloaca. If turtles struck a large stone or root while digging they might abandon their digging effort and move to another site or move back to the water. I never observed a turtle returning to a partially dug nest. *C. expansa* is very tolerant of people during the digging process, on many occasion individuals have completed their nests adjacent to major pedestrian paths with several hundred people walking past them during the nest construction phase. *E. signata* is not so tolerant and most will abandon nesting activity if approached, although some individuals will continue nest construction if the nest is half dug and the observer sits still at a distance of five or more metres away.

The time spent constructing the nest chamber is highly variable and depends on soil water content and compactness. *C. expansa* was observed to take between 20 and 180 minutes and *E. signata* between 30 and 120 minutes. Both species stop digging and begin egg laying once the hole is so deep that the out-stretched hind leg can no longer scoop out soil. Mean bottom nest depth is 12.5 ± 0.5 cm (range 8-16) cm in *E. signata* and significantly deeper ($P < 0.001$) 21.2 ± 0.7 cm in *C. expansa* (range 16-30 cm). In order to maximize the nest depth, *C. expansa* props up on its front legs to increase the stretch of its hind limbs during the final stages of nest construction (Fig. 3). I did not observe this behaviour in *E. signata*.

Egg laying

This process is similar in *C. expansa* and *E. signata*. Egg laying is relatively fast taking 10-20 minutes and eggs are laid one at a time. Typically one foot is left dangling in the nest hole during oviposition (Fig. 4), but after 2-4 eggs are laid this foot is with drawn and the other foot is inserted and this process continues until egg laying is complete. Eggs can be moved by the hind foot coming into contact with them at this time and in some individuals a newly deposited egg is deliberately moved by the inserted foot before another egg is laid. Both species can be approach very closely once egg laying has begun without causing the female to abandon egg laying. *C. expansa* typically lays 10-22 eggs (mean clutch size 16) and *E. signata* typically lays 12-30 eggs (mean clutch size 18).

Figure 3. Front legs propping up the body to allow maximum hind foot reach during the final stage of nest construction in the broad-shelled river turtle *C. expansa*.

Nest filling

Both *C. expansa* and *E. Signata* use alternative movements of their back feet to 'sweep' soil back into the nest cavity once oviposition is complete (Fig. 5). The transition from oviposition to nest filling is typically rapid, nest filling commencing within a minute or two of the last egg being laid. Nest filling continues until the nest neck is filled to the original ground height. This process typical averages 12.2 ± 1.0 min (range 10-20 min) in *E. signata* and significantly ($P < 0.001$) longer 25.2 ± 2.0 (range 20-30 min) in *C. expansa*. The longer period in *C. expansa* is caused by 'body slamming' behaviour in this species. After the soil has been back filled to the original ground level, *C. expansa* lifts the back end of its body off the ground with its hind legs, and then allows its hind legs to collapse

Figure 4. Egg laying in the broad-shelled river turtle *C. expansa*. Note that during egg laying one foot is typically left daggling into the nest.

Figure 5. Back-filling of nest using hind feet to sweep soil into nest hole by *C. expansa*.

which causes the rear end of the plastron to 'slam' onto the nest plug and compact the soil (Fig. 6). This body slamming process is repeated many times before leaving the nest area. I have not observed this body slamming behaviour in *E. signata*.

Return to water

Both *C. expansa* and *E. signata* move more or less in a straight line directly back to the water after they have back filled their nest. In both species the speed of walking back to the water is faster than the walking speed when coming out of the water. *C. expansa* is also much more timid at this stage compared to when it is walking up a hill to nest. If approached it will begin to run down the hill and will attempt to dodge and avoid capture rather than withdraw its head under its shell which is the more typical action then approached when they are walking up the hill to nest.

Discussion

Nesting season

Both Brisbane river turtles (*E. signata*) and broad-shelled river turtles (*C. expansa*) were only ever observed out nesting during or soon after rain. This is a common feature of Australian freshwater turtle nesting (Goode 1965; Goode and Russell 1968; Vestjens 1969; Clay 1981; Kuchling 1993; Cann 1998). Possible reasons why turtles wait for rain include the fact that heavy soils are much easier to dig into when moist and that turtle eggs exchange water with the soil surrounding the nest and wet soils allow eggs to be in a positive water balance and absorb water from the soil and increase their water reserves. If during the incubation period soils dry and eggs fall into a negative water balance situation (i.e. they lose water to the environment) they can call on these water reserves to continue successful development. Freshwater turtles are able to store the mature eggs in the uterus during the nesting season (eggs can remain viable within the uterus for at least three months Goode and Russell (1968)) until suitable rains arrive because the embryos diapause at the gastrula stage of development while being retained within the uterus (Legler 1993). This can result in considerable nesting synchrony amongst individuals once it does rain, especially if there are several weeks in a row when rain does not fall. Because most nest predators such as water rats and monitor lizards use olfactory cues to locate nests, and these olfactory cues fade in the few days after nest construction, synchronous nesting may help 'swap' nest predators and thus increase the chances of eggs surviving nest predation (Moll 1986).

E. signata like most freshwater turtles lay their eggs at a time of year when soil temperatures are increasing or are already warm so that embryonic development begins and is continuous as soon as the eggs are laid. This results in a relative short incubation period (2-3 months), with variation in incubation being caused by differences in incubation temperature of different nests. In contrast, *C. expansa* lays its eggs at a time when soil temperatures are falling and embryos enter a diapause over winter until the soils warm again during Spring (Booth 2002). As a consequence the incubation period of *C. expansa* at St Lucia is long and highly variable (5-10 months), with most of the variability due to differences in laying date which causes differences in the amount of time embryos spend in the diapause phase (Booth 2002).

Nest site selection

C. expansa and *E. signata* for the most part choose different area and different times of the day to construct their nests. *C. expansa* nest during day light and always nest a considerable distance from the water's edge and usually up a hill. Nesting during the day could be a strategy to select thermally more suitable nesting sites, as areas of sun and shade may be determined although on many if not most occasions the sun is obscured by heavy cloud cover during the nesting process. Freshwater turtles in general show a preference for more sun exposed sites to construct nests (Ehrenfeld 1979; Janzen 1994). Given that *C. expansa* eggs have a very prolonged incubation period, nesting up hill along way from the water's edge may be a strategy of minimizing exposure to the risk of nest flooding. If nests become submerged for a period of more than a few hours the embryos will suffocate as the rate of oxygen diffusion through the nest is insufficient to meet the embryo's needs. The down side to nesting a long way from water is that hatchlings emerging from the nest have a long distance to travel before they can enter the water.

E. signata nest primarily at night, a strategy that may decrease the chance of females been taken by predators during nesting. This strategy also decreases the chances of being exposed to fatally high temperatures while out of water. *E. signata* generally nest close the water's edge, so hatching turtles don't have far to travel before entering the water, but this behaviour also increases the chances of nests being submerged during a flood.

Both *C. expansa* and *E. signata* do not appear to select a particular soil type to nest in. They construct nests in soils varying from sandy-loam to heavy clay. Vestjens (1969) noted that *C. longicollis* would nest in all soil types as well. Soil type does not appear to be a major factor in nest site selection process of chelonians (Ehrenfeld 1979).

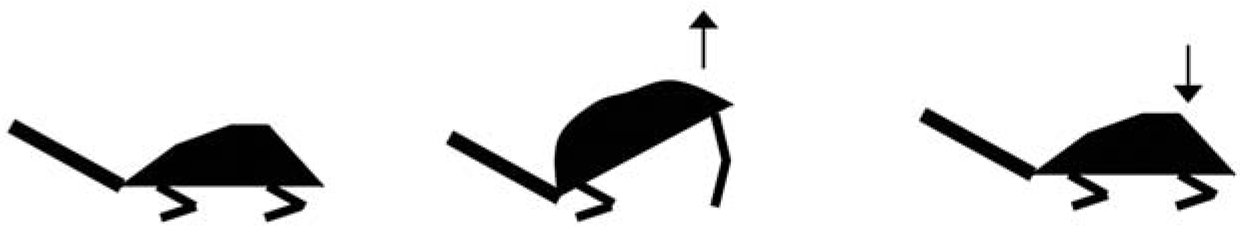

Figure 6. Schematic of the 'body slamming' behaviour displayed by the broad-shelled river turtle (*Chelodina expansa*) at the end of the nest back-filling process.

Nest construction

The nest construction process of *C. expansa* and *E. signata* is very similar to that described for other freshwater turtles (Goode 1965; Goode and Russell 1968; Ehrenfeld 1979; Cann 1998). Both species only use their hind limbs in the digging process, and use the stereotypical one leg at a time scooping behaviour where the webbing is cupped slightly to form the scoop. Each scoop of soil is then deposited to the side of the nesting hole where it remains until the nest backfilling process. Variation in the time taken to dig the nest is caused by how soft the soil is. Wet soil is easier to dig and turtles that nest after the ground has been saturated complete the nest construction process in the least time and this may be one of the reasons why turtles only come out to nest during or after rain. Vestjens (1969) also noted that the time taken to dig a nest depends on the physical characteristics of the soil in the eastern snake-necked turtle (*Chelodina longicollis*). Some *C. expansa* nests were constructed in very heavy clay soils which are near impossible to dig into when dry. Soil moisture content is also important in these nests at the end of incubation as hatchlings cannot dig themselves out of the nest until the clay is softened by rain (Vestjens 1969; D.T. Booth unpublished data).

The rate of hind limb digging movements decreases with time during the nest digging process in both species. When nest construction commences there is little or no pause between alternate limb movements, but by the end of the digging process pauses of between 2-3 minutes between alternate limb movements become common. In clay soil *C. longicollis* rests for periods up to seven minutes while digging the nest cavity (Vestjens 1969). If during nest construction the soil becomes too hard to dig (this sometimes occurs after the first rain of the season when the sub-surface soil remains relatively dry) or a large stone or root is encountered, the female abandons that nest attempt and either moves off to another site or returns to the water. Nesting appears to be an all or nothing event, either the nest is dug to the limit of the hind limb reach and eggs are laid, or if the nest fails to reach this depth eggs are not laid. Abandoned nesting attempts are never back-filled.

E. signata is easily disrupted during the nest construction process, especially when the nest is only a few centimetres deep. They appear to become less likely to abandon their nesting attempt as the nest chamber becomes deeper as if there is a nest effort/fleeing trade off, i.e. the greater effort that has been put into constructing the nest, the more likely they are likely to stick it out and complete the nest. If a female *E. signata* is approached during the latter stages of nest construction, she will stop digging but stay put, only fleeing if the approaching person comes closer than about five metres. In contrast *C. expansa* is very tolerant of human approach during the nest digging phase and frequently constructs nests within two metres of pedestrian pathways where pedestrian pass at the rate of one or two per minute. In one case a turtle dug its nest into an ant colony beside a pedestrian path and the ants covered the turtle biting and stinging it – the turtle appeared to be completely oblivious to the attacking ants. None-the-less, a passing good Samaritan on seeing the ant attack pulled a one litre bottle of water from their backpack and poured the entire volume onto the nesting turtle's head, neck and front legs! The turtle ceased digging momentarily, but them continue on and successfully completed her nest.

Because of the hind leg scooping process used to construct nests by both *C. expansa* and *E. signata*, the nest chamber constructed is usually slightly larger in diameter at is base than at is top, giving the nest a distinct flask-shape which is a common feature of freshwater turtle nests (Goode 1965; Goode and Russell 1968; Vestjens 1969; Ehrenfeld 1979; Georges et al. 1993; Cann 1998). This nest shape has the effect of allowing more eggs to be incubated at the bottom of the nest and to have fewer layers of eggs sitting on top of each other than would occur if the nest was a simple vertical shaft (Fig. 7). The net effect of this is that the majority of eggs are laid deeper in the ground and are exposed to smaller cyclic daily fluctuations in temperature as the magnitude of these cyclic fluctuations decrease with soil depth (Booth 2006). Maximizing nest depth is a common feature of turtles (Ehrenfeld 1979) but appears to be particularly important to species like *C. expansa* that prop themselves up on their front legs in order to increase the reach of their hind legs during the final stage of nest digging.

Although water stored in the bladder and or cloaca may be deposited into the nest during the nest construction process or during egg laying itself (Curtis 1928; D.T. Booth unpublished data), neither *C. expansa* nor *E. signata* was ever observed to make several trips from the water to the nest to deposit water as has been reported to occur in *C. longicollis* (Cann 1988). However, this behaviour was not observed in *C. longicollis* by Vestjens (1969). Indeed, it appears that once a nesting site has been left the female turtle never returns to it. The deposition of fluid from the cloaca onto the nest plug after refilling as described by Cann (1998) and the 'puddles' behaviour in which cloacal fluid is mixed with soil and eggs in clay

Figure 7. View into a *C. expansa* nest after egg laying has been completed but before back-filling has commenced. Note the flask-like shape of nest chamber which allows more eggs to be placed deeper in the soil compared to if the nest chamber had vertical walls.

soils as described by Goode and Russell (1968) were never observed. Deposition of water from the cloaca at some stage during the nesting process is relatively common in freshwater turtles (Ehrenfeld 1979). Whether this water comes from the urinary bladder or is stored in cloacal bursa is unknown.

Egg laying

The egg laying process in *C. expansa* and *E. signata* is similar to that described for other freshwater turtles (Ehrenfeld 1979). Both species leave a limb hanging into the nest during oviposition and as a consequence eggs are spread about the nest chamber floor as a result of this dangling limb coming into contact with them. In some individuals eggs are deliberately moved by the dangling foot after each egg is laid, but in others deliberate egg movement was not seen. Eggs are deposited singly at the rate of approximately one every 30-60 s, but this interval between subsequent eggs can stretch to ~120 s when the daggling limb is withdrawn and the over limb inserted.

Limb daggling behaviour has been reported previously in Australian freshwater turtles (Curtis 1928; Goode 1965; Goode and Russell 1968; Vestjens 1969; Cann 1998) and all these authors indicated that eggs were deliberately moved. Several species of north American freshwater turtle are also reported to manipulate their eggs with their hind limbs during the oviposition process (Ehrenfeld 1979).

In common with other nesting turtles (Ehrenfeld 1979), once oviposition has commenced, both *C. expansa* and *E. signata* enter a trance-like behavioural state where they are not easily disrupted. Even the highly timid *E. signata* can be touched at this stage without the animal fleeing.

Nest back filling

The transition from egg laying to back filling is rapid as is the case in most nesting turtles (Ehrenfeld 1979). Once begun the hind limbs sweep across the ground's surface in rapid succession scraping the spoil previously dug out of the nest back into the nest cavity. In *E. signata* the nest site is abandoned once the soil surface is levelled across the egg chambers top. But *C. expansa* at this stage enters a 'body slamming' behaviour that compacts the soil plug in the neck of the nest. Similar behaviour has been reported previously in several species of Australian freshwater turtles (Vestjens 1969; Goode 1965; Georges et al. 1993) and the eastern red-bellied turtle *Pseudemys rubriventris* from north America (Ehrenfeld 1979). However in these cases all four legs are used to raise the body off the ground before body-slamming. The reason I did not observe this behaviour in *E. Signata* may be that my close proximity to the nesting female caused them to leave the nest site prematurely as this population is very sensitive to human presence. The compaction of the nest plug through body slams may act as a nest predator deterrent as the nest plug is very difficult to remove in clay soils.

Summary

In summary the entire nesting procedure from leaving the water until re-entering the water can vary between one and four hours in both *C. Expansa* and *E. signata* similar to previously reported nesting times (Curtis 1928; Goode 1965; Goode and Russell 1968; Vestjen 1969; Cann 1998). The variation in nesting time is due to both the distance travelled to the nesting site and the difficulty of digging into the soil. The behaviour of water being dumped into the nest from the cloaca and the manipulation of eggs with the back legs after they have been deposited into the nest is worthy of closer investigation. Details of what goes on inside the nest at this egg deposition stage are difficult to determine because the back of the turtle is usually obscuring a clear view of the nest's chamber. *C. Expansa* could be a good species to study in this respect as it nests during the day and is very tolerant of close observation.

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